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Correlations between species richness and exposure: Freshwater molluscs and macrophytes

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Abstract

I measured the correlation between a major environmental gradient in Inner Long Point Bay, Lake Erie, and the species richness of macrophyte and mollusc communities. This gradient of wind and current induced exposure in the benthic habitat was negatively correlated with macrophyte species richness ($r = -0.68$, $p < 0.001$), positively correlated with richness of the fingernail clam guild ($r = 0.58$, $p < 0.001$), and uncorrelated with the snail ($r = 10$, $p = 0.53$) and filter-feeding mussel ($r = 0.18$, $p = 0.27$) guilds. Two models to explain the observed correlations are presented and compared. The "accelerated/retarded trajectory" model predicts that a disturbance such as exposure will either accelerate or retard the movement of a community to a general equilibrium, depending on the selectivity of the disturbance. The "gradient of equilibria" model postulates changes in the competition coefficients themselves with increasing disturbance, ultimately causing variation in species richness.

Introduction

Ecologists have long searched for some explanation of variation in species richness. Why do some habitats support numerous species of the same guild while others are relatively depauperate? It is commonly held that if a community is at "competitive equilibrium" (Huston, 1979) and there is no shortage of colonizing species, there will be as many species present as can be accomodated by the niche space (abundance and diversity of resources) available. However, predation or abiotic disturbance may act to keep population sizes below the "niche controlled" equilibrium densities and thereby reduce the intensity of competition in the community. Richness has often been observed to increase in response to such "intermediate disturbance" (e.g. Connell, 1970, 1978; Dayton, 1971; Menge, 1976; Paine, 1966, 1971,

1974; Keddy, 1983, 1984.

Yodzis (1978, 1985) argued that the effect of an intermediate level of disturbance on species richness depends on both the nature of the community and the selectivity of the disturbance. As an example, he cites both theoretical (Yodzis, 1977) and empirical (Addicott, 1974; Risch & Carroll, 1982) evidence for the hypothesis that species richness actually declines in niche controlled communities exposed to nonselective disturbance.

Niche controlled communities probably represent the traditional view of how communities are structured. But Yodzis (1978) also defined two kinds of communities (dominance and founder controlled) particularly relevant to benthic plans and animals. Species can co-exist in such systems without niche differentiation because of pure competition for space. Dominance controlled communities are those

where the species compete for space and there is some, possibly cyclical hierarchy of ability to occupy and displace others from the space. Species in founder controlled communities also compete only for space, but the "winner" of a given piece of space is determined largely by which species occupies it first. This is primarily a function of the relative speed of colonization of the member species.

Yodzis' (1978, 1985) predictions of the effects of disturbance on each of these community types basically reflect either an acceleration or a retardation of a community's movement to equilibrium. If disturbance selectively impacts sub-dominants, they are eliminated more quickly from the community and lower richness results. If disturbance primarily impacts the dominant species, elimination of subdominants is prevented or retarded and increased richness results. I will call this an "accelerated trajectory" or "retarded trajectory" model of varying richness, depending on the impact of the disturbance.

Another possible cause of variation in species richness along a disturbance gradient is covariability of the competition coefficients with the disturbance. A single dominant species in a habitat with little disturbance may be a poor competitor in more disturbed areas. Its replacement by several species in habitats with significant disturbance may mimic the predictions of Yodzis' model, but the changes in richness would be the result of new equilibrium points along the disturbance axis rather than accelerated or retarded movement to a general equilibrium. I will call this a "gradient of equilibria" model.

In this study I measured the relationship between an environmental gradient of disturbance (wind and current induced turbulence or "exposure" in Inner Long Point Bay, Lake Erie) and the species richness of freshwater molluscs and aquatic macrophytes in the bay. I will show that both of the models described are consistent with the data, and I will propose experiments which will increase our understanding of how species richness varies in these communities.

Materials and methods

In June, 1984, 11 transects were sampled by boat in Inner Long Point Bay, Lake Erie (Fig. 1; 42°38'N; 80°24'W). Every kilometre along a transect the boat
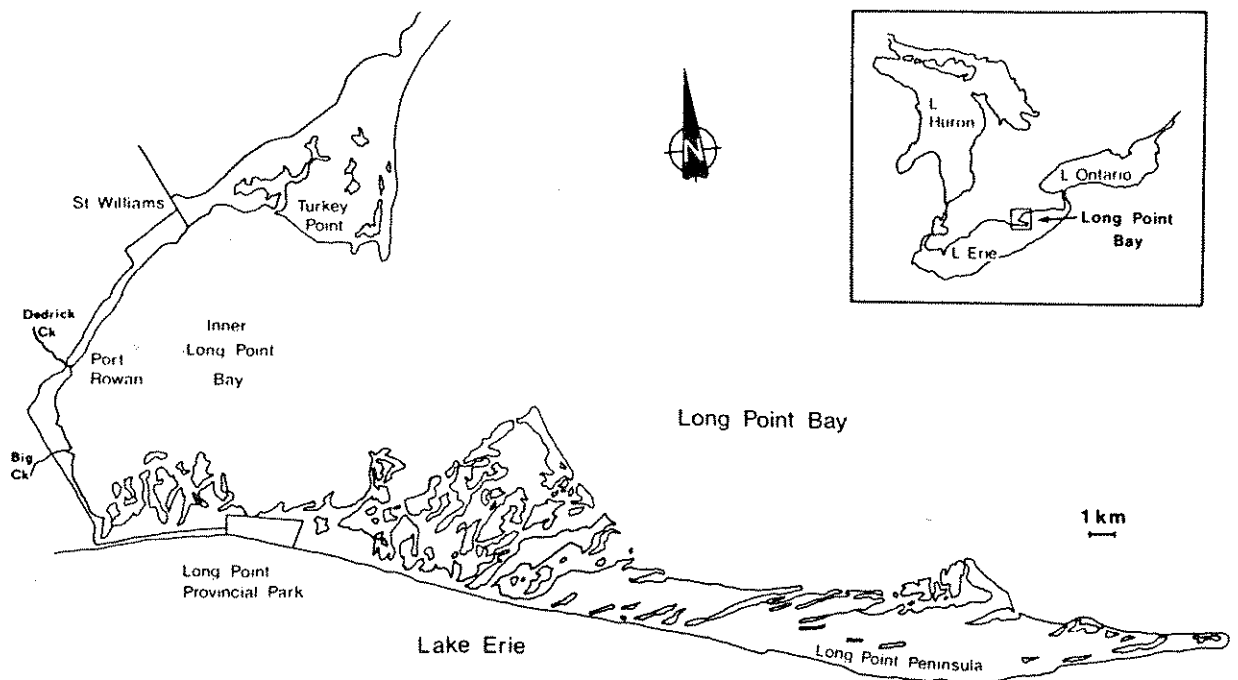

Fig. 1. The study area.

was anchored and a sampling site was established. The transects were chosen in an effort to equally allocate the sites to near (< 1 km) and offshore areas. A total of 41 sites were sampled.

At each site a plastic, circular sampling frame (i.d. = 1 m) was used to sample three randomly chosen subsites within 5 m of the boat. I used SCUBA at each of the subsites to measure depth, hand-collect all mussels in the frame area, collect or site-identify macrophytes, take two sediment samples for small molluscs and sediment analyses respectively, and collect a water sample in a Pyrex stoppered bottle. All samples were placed in a cooler immediately.

Within 12 h the mussels were cleaned and identifies, one sediment sample from each subsite was sieved and hand-picked for small molluscs (which were preserved in 40% ethanol), reference macrophytes were placed in a plant press, and the water samples were processed. The pH was measured with a Fisher Accumet pH meter (Model 156). Alkalinity and calcium were determined titrimetrically as described in ASTM (1978).

Analyses of sediment samples from each subsite were done over a two month period, so the samples were kept frozen until analysis. Loss on ignition (LOI) of the sediments was estimated by drying a sample at 80 C, cooling, weighing out a small (< 25 g) subsample, baking at 550 C for one hour, cooling, and reweighing. LOI was the proportion of weight lost during the baking process. Sand content was the percentage of a dried, 250 g subsample of the sediment which did not pass through a 74 micron (No. 200) sieve after wet sieving. No sediments contained any particles larger than coarse sand.

Macrophyte identifications were made using Fasset (1975), Prescott (1962), and Gleason and Cronquist (1963). Mussels (Unionidae) were identified using Clarke (1981) and were verified by J. M. Topping (Nat. Mus. Canada). Clarke (1981) and Mackie *et al.* (1980) were used to identify the gastropods, and G. L. Mackie (University of Guelph) identified or verified the Pisidiidae.

Environmental and biological data for each site were obtained by pooling data from the three subsites. Thus, if a species occured in only one of the three subsites at a particular site, it was considered

"present" at that site. For each environmental variable, the mean of the three subsites was used to represent the site.

The major environmental gradient in the bay was determined using principal component analysis (PCA; using SAS PROC PRINCOMP [SAS Institute 1985] on the covariance matrix of the log-transformed (except for pH) environmental data (alkalinity, calcium, pH, depth, % sand, LOI). These variables adequately reflect both the water and sediment quality at each site, and are temporally stable relative to other possible descriptors. Log transformations were used to improve the linearity of relationships among the variables. Pearson correlations and scatter plots were used to assess the strength and nature of the relationship between the score of a site on the major environmental gradient (i.e. the first principal component) and the species richness of the three molluscan guilds (grazing gastropods, filterfeeding mussels, deposit-feeding fingernail clams). The relationship between the environmental gradient and macrophyte species richness was also examined by the same procedure.

Results

Substrate characteristics of Inner Long Point Bay were much more variable among the sites than either water chemistry or depth (Table 1). This is also indicated in the results of the PCA (Table 2; Fig. 2), which showed only one meaningful gradient in the environmental data: mucky (low % sand, high LOI) to sandy (high % sand, los LOI) sites. I will interpret this as a gradient of "exposure", or wind and current

Table 1. Means, ranges, and coefficients of variation of environmental variables (n = 41).

	MEAN	RANGE	C.V.
Alkalinity (meq L^{-1})	2.34	1.89 – 2.99	13
Calcium (mg L^{-1})	39.4	32.7 – 50.0	12
pH	8.4	8.2 – 9.0	2
Depth (m)	2.53	1.17 – 3.70	22
% Sand	50.0	2.4 – 99.2	68
% L.O.I.	2.5	0.3 – 6.3	70

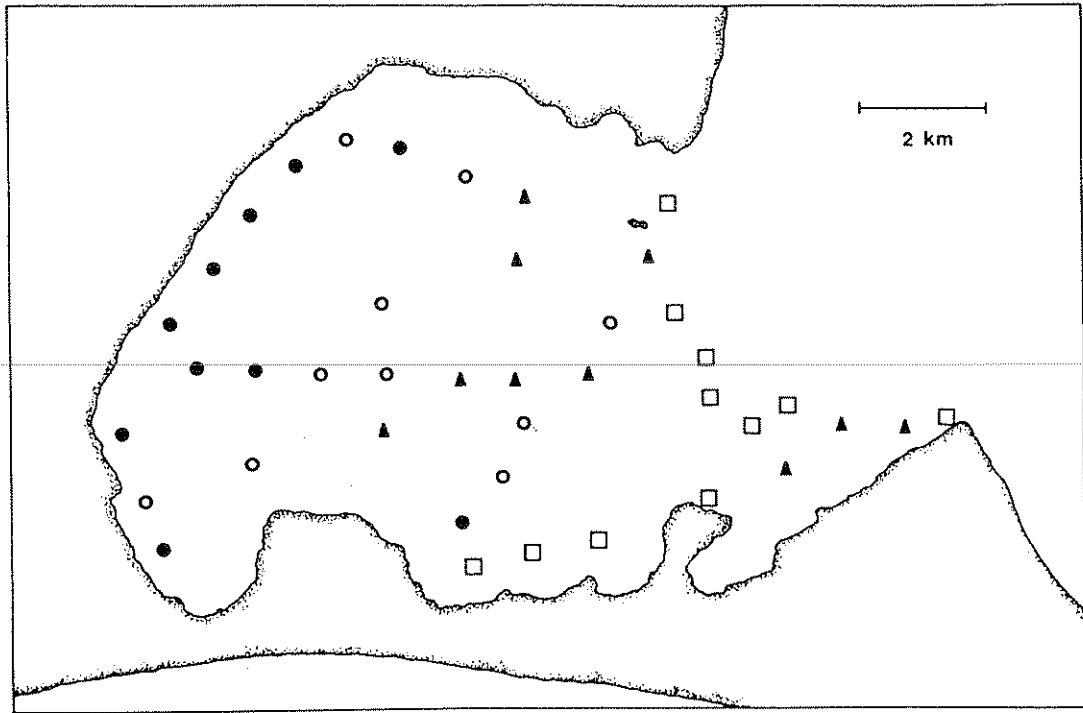*Fig. 2.* Quartiles of sites on the exposure gradient as measured by their PC1 scores (□ = very high; ▲ = high; ○ = medium; ● = low).

Table 2. Principal component analysis of the log-transformed (except pH) environmental data.

	Eigenvectors		
	PC1	PC2	PC3
Alkalinity	−0.08	−0.04	−0.20
Calcium	−0.07	−0.04	−0.06
pH	0.06	−0.12	−0.12
Depth	−0.06	0.16	0.95
% Sand	0.80	0.59	−0.07
L.O.I.	−0.58	0.78	−0.18
Eigenvalue	1.16	0.08	0.06
% Explained	87	6	5

Table 3. Macrophyte species and frequencies.

Species	Frequency (out of 41 sites)
Anacharis canadensis (Michx.) Rich.	8
Ceratophyllum demersum L.	5
Chara vulgaris L.	27
Myriophyllum spicatum L.	12
Najas flexilis (Willd.) Rostk. & Schmidt	13
Nitella flexilis (L.) C.A. Agardh	1
Potamogeton illinoensis Morong.	1
Potamogeton crispus L.	1
Potamogeton filiformis Pers.	1
Potomageton gramineus L.	1
Potamogeton pectinatus L.	1
Potamogeton praelongus Wulfer.	10
Vallisneria americana Michx.	26

induced turbulence in the benthic environment.

I found 14 species of macrophytes in the bay (Table 3). *Chara vulgaris* and *Vallisneria americana* were the two most common species. Three distinct guilds of molluscs were found (Table 4). There were nine species of snails (Gastropoda) present, with *Amnicola limosa* and *Pleurocera acuta* each occur-

ing in over half of the sites. The most frequently occuring mussels (Unionidae) of the ten species found were *Lampsilis radiata* and *Anodonta grandis*. Of the 14 fingernail clam (Pisidiidae) species present, *Pisidium nitidum* was clearly the most common.

Table 4. Mollusc species and frequencies.

Species	Frequency (out of 41 sites)
GASTROPODA (snails)	
Amnicola limosa (Say, 1817)	24
Campeloma decisum (Say, 1816)	3
Helisoma trivolis (Say, 1816)	1
Marstonia decepta (Baker, 1928)	1
Physa gyrina Say, 1821	7
Pleurocera acuta Rafinesque, 1831	24
Pseudosuccinea columella (Say, 1817)	1
Valvata sincera Say, 1824	6
Valvata tricarinata (Say, 1817)	7
UNIONIDAE (mussels)	
Anodonta grandis Say, 1829	13
Anodonta imbecilis Say, 1829	3
Ellipto dilatata (Rafinesque, 1820)	3
Fusconaia flava (Rafinesque, 1820)	2
Lampsilis radiata (Gmelin, 1792)	23
Lampsilis ventricosa (Barnes, 1823)	2
Ligumia nasuta (Say, 1817)	10
Pleurobema coccineum (Conrad, 1836)	1
Proptera alata (Say, 1817)	3
Villosa iris (Lea, 1830)	1
PISIDIIDAE (fingernail clams)	
Musculium lacustre (Muller, 1774)	3
Musculium partumeium (Say, 1822)	11
Musculium transversum (Say, 1829)	9
Pisidium casertanum (Poli, 1795)	12
Pisidium compressum Prime, 1852	10
Pisidium equilaterale Prime, 1852	1
Pisidium lilljeborgi Clesson, 1886	3
Pisidium nitidum Jenyns, 1832	21
Pisidium rotundatum Prime, 1852	5
Pisidium subtruncatum Malm, 1855	3
Pisidium variabile Prime, 1852	5
Pisidium ventricosum Prime, 1851	1
Shaerium corneum (Linnaeus, 1758)	9
Sphaerium striatinum (Lamark, 1818)	2

Table 5. Means, ranges, and correlations with exposure of macrophyte and mollusc species richness (n = 41).

	MEAN	RANGE	EXPOSURE 'r'
Macrophytes	2.6	1 – 6	– 0.68***
Snails (Gastropoda)	1.8	0 – 4	0.10[NS]
Mussels (Unionidae)	1.5	0 – 4	0.18[NS]
Fingernail Clams (Pisidiidae)	2.3	0 – 9	0.58***

(***: p < 0.001, NS: p > 0.25)

Although other macrobenthos (i.e. insects, crustaceans) were found, they were not identified. The molluscs were clearly dominant both numerically and with respect to biomass.

The species richness of the macrophytes and the three molluscan guilds are presented in Table 5, together with their correlations with the exposure gradient (as defined by the PCA). The macrophyte and fingernail clam assemblages have strong, opposite correlations with the exposure gradient (Fig. 3). The nature of these correlations was clarified by comparing the five most exposed sites, with a mean LOI of 0.6% (range of 0.29 to 0.69%) and a mean % Sand of 94.9% (82.5 – 99.2%), to the five least exposed sites, with a mean LOI of 4.3% (3.1 – 5.7%) and a mean % Sand of 9.2% (6.6 – 11.4%).

The five lowest exposure sites had a mean of 0.6 (0 – 1) fingernail clam species and a mean of 3.8 (3 – 5) macrophyte species. The only pisidiid species found at these sites were *M. partumeium, P. nitidum,* and *P. compressum.* Four of the five lowest exposure sites had *Anacharis canadensis, Najas flexilis, Vallisneria americana,* and *Myriophyllum spicatum.*

The five highest exposure sites had a mean of 3.6 (2 – 8) pisidiid species and 1.8 (1 – 3) macrophyte species. *Chara* was the only macrophyte present in all five high exposure sites, and it occurred alone in two of these five sites. Of the fingernail calms, *P. casertanum* occurred in four of the five sites, but no other species occurred in more than two of the five sites.

Discussion

The exposure gradient

The fine sediments of Inner Long Point Bay originate as deltaic deposits of Big Creek and Dedrick Creek, the primary inflows (Heathcote, 1981), with some contribution from decomposing macrophyte and plankton debris. The position of a site on the "exposure" gradient defined in this study depends on the sources, transport, re-suspension, and accumulation of this fine material. This is determined by the location of the primary inflows (the southwest
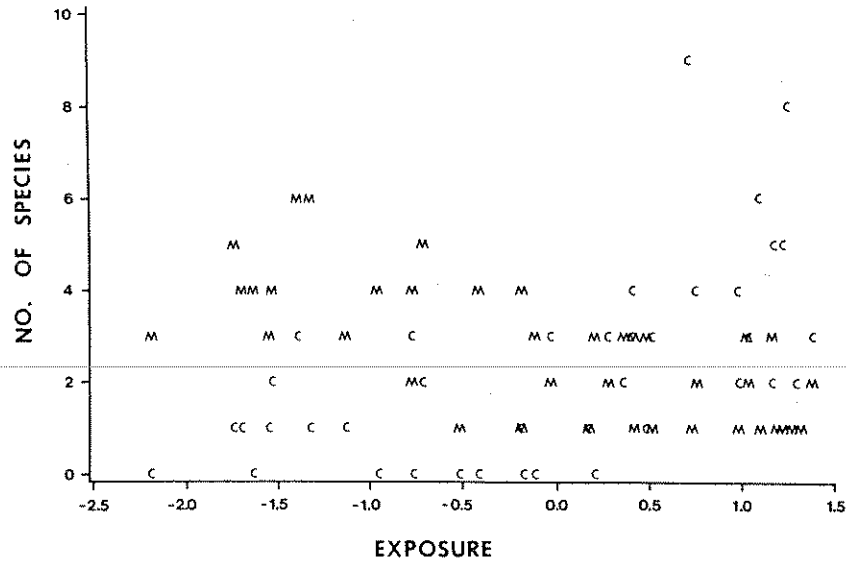
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Fig. 3. Species richness of macrophytes (M) and fingernail clams (C) in relation to exposure (the score of each site on the first principal component of the environmental data).

corner of the bay; Fig. 1) and the prevailing winds, which are from the southwest (Kohli & Farooqui, 1980). Wind-induced shallow waves (Wetzel, 1975) will cause increasing benthic turbulence as one moves away from the southwest shoreline. These winds also generate surface seiches, with amplitudes as high as 2 m in Lake Erie (Wetzel, 1975), which will "flush" the part of the Inner Bay not protected by Turkey Point (the norhteastern gate of the bay) on a southwest/northeast axis. Considered together, these factors explain the distribution of high, medium, and low exposure sites in Inner Long Point Bay (Fig. 2).

The macrophyte community

Chara vulgaris appears to be functionally dominant at sites with high exposure, perhaps because it is better able to maintain attachment in more turbulent areas than other species. It is also much less reliant on nutrient uptake through roots than the angiosperms, so less organic sediments do not hinder its growth. Wilson and Keddy (1986a) argued that macrophytes with small rosettes are more resistant to wave damage than those with tall, leafy shoots,

and thus are better competitors at high exposure sites. *Chara,* with its low-lying stalks and finely divided "leaves" also appears to be morphologically adapted to more turbulent habitats. In less exposed sites it may suffer from shading by the taller, broader-leafed species.

Thus, the correlation between species richness and exposure found in Inner Long Point Bay may have been caused by a "flip-flop" in competitive superiority as exposure increased (the "gradient of equilibria" model). When measured in an undisturbed, organic-rich habitat, macrophyte species from low exposure areas had greater competitive ability than those from high exposure sites (Wilson & Keddy, 1986a). But relative competitive ability may vary substantially if measured at different points along the disturbance gradient. Wilson and Keddy's results may have been different had their experiment been repeated in a more disturbed habitat.

Alternatively, the leafy macrophytes may be considered functional dominants that are selectively impacted by increasing wave exposure. Such a disturbance should enable sub-dominants to maintain a presence and species richness to increase (Yodzis, 1985). Wilson & Keddy (1986b) observed a decline in diffuse competition among macrophyte species

with increasing exposure, which would support such a "retarded trajectory" model. The reduction in richness observed in the present study may just represent "excessive" rather "intermediate" disturbance, and the inability of species other than *Chara* to resist local extinction at high exposure. Peaks in species richness at an intermediate level of exposure have been observed in shoreline macrophyte communities (Keddy, 1983, 1984).

The fingernail clam community

There is evidence that both niche differentiation and dominance hierarchies help to structure fingernail clam communities. *Sphaerium* and *Musculium* species are epifaunal, while *Pisidium* spp. are infaunal, so these two groups may coexist in a given patch by niche differentiation. A field experiment has shown that interspecific competition between congeneric species of the Pisidiidae occurs, and may be more important than intraspecific competition (Mackie *et al.*, 1978; Connell, 1983).

Mackie *et al.* (1978) found *Musculium transversum* to be competitively superior to *M. securis* in shallow water, and predicted that *M. transversum* would eventually eliminate *M. securis* in similar habitats if they occurred together. In deeper waters they found no evidence of inter-specific competition. In this study *M. transversum* was numerically dominant in areas of low exposure. If it is functionally dominant in these areas, perhaps its numbers are sufficiently reduced at high exposure for other species to coexist. Either physical disturbance or increased predation by waterfowl in the exposed areas (Smith, 1979) may cause such a reduction in *M. transversum*. Richness would be higher in the more exposed areas, as predicted by the "retarded trajectory" model.

Alternatively the exposure gradient may be correlated with changes in the dominance hierarchy, effectively removing M. transversum as a top competitor at high exposure, increasing the proportion of contingent competitive interactions (Yodzis, 1985), and thereby increasing richness.

Non-significant correlations: Snails and mussels

The species richness of two molluscan guilds (the snails and the mussels) showed no relationship with the exposure gradient. This was unexpected for the snails because plant richness was highly correlated with the gradient and macrophytes are an important component of the feeding and habitat niche of the gastropods. MacArthur & MacArthur (1961) found that with increasing structural diversity of the vegetation, the diversity of birds using the vegetation increased. The lack of such a relationship in my data may indicate i) lack of real structural diversity in the macrophyte species or ii) broad niches with respect to macrophyte preference in the snails. I would tentatively reject the first hypothesis because of the diverse morphology of the macrophytes found. The second explanation seems more likely, in which case the exposure gradient is likely having little general effect on the life habits of the gastropod guild. The mussels (Unionidae) appear to have adequate within-species plasticity (e.g. Hinch *et al.*, 1986) to be similarly well-buffered from the exposure gradient, at least at the community level.

Choosing a model: Beyond correlational data

Both the "retarded trajectory" and the "gradient of equilibria" models have been used to explain the observed correlations between species richness and exposure. The predominance of one or the other in explaining field observations depends on one's knowledge of the competitive interactions in a community at various points along a disturbance gradient. In particular, the relationship between diffuse competition and the level of disturbance must be evaluated experimentally (e.g. Wilson & Keddy, 1986b). If competition is important at intermediate levels of disturbance, changes in the dominance hierarchy with variation in disturbance must be measured. If it is relatively unimportant, then the selectivity of the disturbance and the availability of hardy species will determine the effect of the disturbance on species richness, as predicted in the "accelerated/retarded trajectory" model. Competition may even be of little importance when disturbance (as de-

fined here) is minimal. Thus, although the data are consistent with both of the "competition-based" models discussed, neither may be an appropriate description of the system. The available evidence suggests that for macrophytes, diffuse competition is important at low levels of shoreline exposure, but reduced at higher levels (Wilson & Keddy, 1986b), supporting the "retarded trajectory" model. Although the same may be true for the finernail clam community, clear evidence is lacking.

Summary

Two communities in Inner Long Point Bay, Lake Erie showed strong, opposite correlations between species richness and exposure or turbulence in the benthic habitat. Macrophyte richness was negatively correlated ($r = -0.68$, $p < 0.001$) with exposure, while fingernail clam richness was positively correlated ($r = 0.58$, $p < 0.001$) with the same gradient. Two models, one which predicts changes in richness as a result of a disturbance-caused decline in the importance of competition, and one which predicts the same changes as a result of a disturbance-caused change in competition coefficients, are used to explain the data. Tests for determining which (if indeed either) of these models is appropriate are proposed.

Acknowledgements

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